Latitudinal and altitudinal patterns of the endemic cacti from the Atacama desert to Mediterranean Chile

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ABSTRACT

In this study we describe the biogeographic patterns of the endemic cacti from the Atacama Desert to the Mediterranean area of Chile. Our goals were: (1) to identify areas of high endemism, (2) to test Rapoport's rule, (3) to test the geometric constraints hypothesis, (4) to explore temperature and precipitation as explanatory variables of species richness. We used a list of 72 species of cacti, ranging from 18° to 36° S and from 0 to 4500 m.a.s.l. A Bayesian analysis of Endemicity (BAE) was used to evaluate hierarchical relationships of endemism between different latitudinal bands. Rapoport's rule was evaluated by examining the relationships between latitudinal/altitudinal mid-point, latitudinal/altitudinal range extent and species richness. The geometric constraints hypothesis was tested by examining the existence of mid-domain effect. The BAE indicated two areas of endemism: (1) the northern area between 18° S and 26° S, and (2) the southern area between 27° S and 36° S. The shape of the latitudinal gradient is non-linear, supporting the geometric constraints hypothesis. Altitudinal patterns, however, support Rapoport's rule; a peak of endemism was found at low altitudes. The explanatory variables were elevation, minimum temperature of the coldest month, mean temperature of wettest quarter and annual precipitation.

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1. Introduction

The increase in species richness from the poles to tropical areas is one of the oldest and broadest patterns documented in ecology (Brown and Lomolino, 1998; Willig et al., 2003). Furthermore, the decline in species richness with altitude and a humped pattern with a richness peak at intermediate elevations are also widely accepted (Colwell et al., 2009; McCain, 2004; Rahbek, 1995; Stevens, 1992). However, neither latitude nor altitude by itself is a direct driver of species richness, as these differences are related to latitudinal or altitudinal covariates (e.g. precipitation, temperature, area). Indeed, strong statistical support of contemporary climate control of large-scale biogeographic patterns is a widespread and accepted conviction (Hawkins et al., 2003).

Rapoport's rule and geometric constraints are major hypotheses that have been invoked as causes for latitudinal and altitudinal gradients. Rapoport's rule predicts that environmental gradients can produce selective pressures, resulting in decreased species richness and increased distribution range towards the poles and mountain peaks because only organisms with broad climatic tolerances will be favoured by natural selection in these areas (Rapoport, 1979; Stevens, 1989, 1992; Willig et al., 2003). Latitudinal evaluations have demonstrated that Rapoport's rule is not always satisfied in the Southern Hemisphere (Mourelle and Ezcurra, 1997a). However Rapoport's rule indeed applied to bathymetric patterns of southern polychaetes (Moreno et al., 2008) and to elevation gradients in vertebrates (McCain, 2009). Whether the rule applies to elevation gradients in southern plant groups is unknown. Geometric constraints of geography are also known to affect biodiversity patterns, resulting in the mid-domain effect, in which the random placement of species' ranges within a hard-bounded geographic domain generates a peak of species richness near the centre of the altitudinal or latitudinal domain (Colwell and Hurtt, 1994; Grytnes and Vetaas, 2002). These two hypotheses produce different predictions of the shape of species richness curves: Rapoport's rule predicts a monotonic decrease along the altitudinal and latitudinal domain, while the geometric constraints hypothesis predicts a hump-shaped pattern.

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However, Rapoport's rule and geometric constraints can operate simultaneously, because of the complex interaction with other explanatory variables, thus varying their explaining power between latitudinal, altitudinal or bathymetric species richness patterns (Currie and Kerr, 2008; Colwell et al., 2009).

The Atacama Desert and Mediterranean Chile are distinctive biogeographical provinces (Cowling et al., 1996; Rundel et al., 1991); they offer unique opportunities to test biogeographic hypotheses of species richness gradients, because they occur within the South American Arid Diagonal and the Andes Range, two major geological and climatic formations that produce both environmental gradients and hard geographic boundaries. Furthermore, the western slope of the Andes Range in Chile is longitudinally oriented and narrow, reducing possible geographic area effects. The Arid Diagonal is a belt that crosses South America diagonally from the northwest to the south-eastern slopes of the Andes Range (Houston, 2006), producing environmental gradients that affect precipitation regimes, primary production and seasonality, which increase with latitude (Arroyo et al., 1988; Luebert and Pliscoff, 2006). This gradient can be easily observed in the change of arid vegetation zones from the northern deserts to the rainy temperate forests in southern Chile. Additionally, the Andes Range produces elevation gradients that lead to extreme climatic conditions characterised by a decrease in temperature, an increase in solar radiation and winds and shorter growing seasons (Stevens, 1992). Alternatively, the Arid Diagonal in the north, the Andes range in the east and the southern temperate forests of Chile may act as hard geographic boundaries to arid and tropical latitudinal species distributions. Finally, two other geographic constraints may be relevant, i.e. the coastline and the crest of the Andes; these may act as hard barriers affecting species richness patterns.

The relation of species richness gradients and endemic richness are critical to our understanding of the diversification of specious groups (such as Cactaceae). Species richness and endemism are expected to be coupled when they are shaped by the same isolation mechanisms (Vetaas and Grytnes, 2002). The endemism and species richness of Chilean cacti are one of the highest in the Chilean angiosperm families (Hoffmann and Walter, 2004; Hunt et al., 2006; Marticorena, 1990). All endemic cacti are exclusively distributed between 18° S and 36° S within the Chilean portion of the Arid Diagonal, suggesting that environmental gradients and hard geographic boundaries affect endemism patterns.

Quantitative biogeographical patterns for endemic Chilean cacti have not been studied in depth, in contrast to other countries such as Argentina and Mexico (Goettsch and Hernández, 2006; Hernández and Bárcenas, 1995, 1996; Mourelle and Ezcurra, 1996, 1997a,b). This consequently challenges our understanding of the speciation processes linked to the Arid Diagonal formation, achieving accurate predictions for the plant species of arid zones, consequences of global climate change and the creation of effective conservation initiatives (Hernández and Bárcenas, 1996). Lessons from Argentinean biogeographic patterns showed that Cactaceae richness is linked to favourable temperature and precipitation conditions (Mourelle and Ezcurra, 1996) and Rapoport's rule does not hold for latitudinal patterns in Argentinean cacti (Mourelle and Ezcurra, 1997a).

In this study we describe the biogeographical patterns of the endemic Chilean cacti, evaluating the role of the geometric constraints and Rapoport's rule hypotheses. Also we evaluated the role of climatic variables in determining latitudinal and altitudinal patterns of richness. In particular, our goals were (1) to identify areas of high endemism; (2) to test Rapoport's rule; (3) to test the geometric constraints hypothesis; and (4) to explore temperature and precipitation as explanatory variables of species richness.

2. Material and methods

2.1. Taxonomic database

The database used in this study consists of a list of 72 of endemic Chilean species of Cactaceae (see Electronic Supplementary Material 1,2). All the information is based on herbarium collections (CONC, SGO) and an exhaustive literature inspection. Although data obtained from herbarium collections and specific literature may be influenced by sampling effects, this potential problem is limited because the species of cacti have very narrow distribution ranges, reducing the possibility of unknown distribution limits. We also complemented literature and herbarium data with extensive field explorations. The literature employed in the analyses and amount of data per species can be accessed in Electronic supplementary material 3 and 4, respectively.

2.2. Bayesian analysis of endemicity (BAE)

We performed an analysis of endemicity *via* the Markov Chain Monte Carlo method within a Bayesian framework (hereafter BMCMC). This procedure is similar to the Parsimony analysis of endemicity (PAE, Morrone, 1994). Both BAE and PAE are analogous to phylogenetic hypothesis reconstruction; these approaches classify areas (analogous to taxa) by their shared endemic taxa (analogous to characters). BAE and PAE data consist of area × species matrices, and the resulting phylograms represent nested sets of areas in which the terminal branches of the area phylograms represent a single band of endemism (Morrone, 1994). The matrix for this study was prepared by coding taxa as absent (0) or present (1) in each 1° southern latitude band. Trees were rooted by a hypothetical area coded exclusively with zeros (called "latitude 17° S"), since species presence must be regarded as derived and species absence as primitive.

In the BMCMC, the Bayesian statistical procedure uses the empirical data (observations) to update a prior probability distribution to a posterior probability distribution (Ronquist, 2004). Posterior probability distributions are sampled by a Markov chain Monte Carlo method in order to obtain a stationary and most credible condition (see Ronquist, 2004 for details). Likelihood values and hypotheses of area relationships were generated using the M2P model with no reversible time (directional) implemented in the software BayesPhylogenies (Pagel and Meade, 2004). The M2P runs with presence/absence data with a non-time-reversible (i.e., directional) model, allowing the rates of change from 0 to 1 to differ from the rate of change from 1 to 0 (see BayesPhylogenies Manual, p. 5). In our study this corresponds to the number of species gained along lineages (i.e. branches of the tree) resulting from ecological processes of immigration and/or an evolutionary process of speciation. Approximately 9000 trees were generated using the BMCMC procedure, sampling every 1000th tree to assure that successive samples were independent. We graphically detected the convergence zone of the Markov Chain by plotting trees and their likelihood values, and then removing all trees sampled before the convergence zone (Pagel and Meade, 2004).

2.3. Latitudinal/altitudinal patterns of species richness and distribution ranges of species

We characterised the latitudinal patterns of species richness and distribution ranges of species based on a binary presence/absence matrix. The sum of elements along a row (i.e., latitudinal bands where the species is present) is the distributional range of a species, and the sum of elements along a column (i.e., number of species